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TEMPERATURE REGULATION AND OXYGEN CONSUMPTION IN THE DEVELOPING MACROPOD MARSUPIAL *SETONIX BRACHYURUS*

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SUMMARY

1. When kept at ambient temperatures of 17·5 and 24° C the colonic temperatures of joeys younger than 166 days declined to near ambient temperature. Pouch joeys of 166 days and older were however able to maintain their colonic temperatures at about 35° C.

2. Joeys first developed the ability to sustain high O_2 consumption rates in response to cooling, when aged between 144 and 169 days. Only when this latter facility was fully developed in ontogeny could body temperature be maintained in a cool environment.

3. When joeys older than 130 days were kept in a metabolism chamber at pouch temperature (37·5° C) and at high humidity their body temperatures quickly rose to lethal levels, demonstrating the need for cooling mechanisms whilst still contained within the pouch.

INTRODUCTION

Setonix brachyurus, better known in Western Australia by its aboriginal name the 'quokka', is a small herbivorous marsupial found wild only in south-western Australia. Pouch joeys of these animals first develop the ability to raise their O_2 consumption rates in response to cooling when they are about 100 days old. At 185 days *post partum* when they leave the pouch permanently, a definite thermal neutral zone is established (Shield, 1966). During this 85-day interval the animal changes from one with the characteristic O_2 consumption pattern of a poikilotherm to one with that of a homoeotherm. Homoeothermy also implies, however, a metabolic capability sufficient to sustain heat production at the level required to maintain a high body temperature in a cool environment. It seemed appropriate, therefore, to study the development of the ability of the

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quokka to sustain high O_2 consumption rates in a cool environment and to associate this change with the parallel development of its ability to maintain body temperature over periods ranging from a few hours to several days. We have also studied the change in the level of body temperature of the quiescent joey with time (over several hours) at various stages of development when denied access to heat sinks. This was done to confirm the increasing importance of a means of losing heat during later pouch development.

METHODS

Setonix brachyurus is a small macropodid marsupial weighing between 2·5 and 4·5 kg. The adult female gives birth to one pouch young or joey at each pregnancy after a gestation of between 25 and 28 days. The new-born joey weighs only 0·4 g and will spend about 185–195 days in the pouch during which period it grows to about 500 g (Shield, 1968).

The ages of all joeys were estimated from their body weights, and pes and tail measurements according to a method established by Shield & Woolley (1961). Thirty-four joeys aged between 48 and 192 days were used in the body temperature measurements and a separate group of thirty-six animals aged between 11 and 186 days was used only for the O_2 consumption measurements. This latter group was divided into two sets each containing eighteen joeys of comparable age-distribution. Joeys assigned to each set were selected so that they were in six age groups. These groups represented the subdivision of the 185 days of pouch occupancy into five periods of 30 days each and a terminal period of 36 days.

Colonic and pouch temperatures of adult females and colonic temperatures of their pouch joeys were measured with a 0–50° C mercury-in-glass thermometer with 0·1° C division. Colonic temperatures of joeys in the metabolism chamber were measured with a small plastic covered thermistor inserted into the rectum to the level of the colon. Ambient temperature in the metabolism chamber was measured with a similar thermistor fixed about 50 mm from the flanks of the animals. Thermistor temperatures were read by a telethermometer with an accuracy of ± 0·1° C and recorded on a strip chart recorder. O_2 consumption was measured in a thermobarometer apparatus previously used and described by Shield (1966). Body temperatures and O_2 consumption measurements were made in metabolism chambers kept within ± 0·5° C of the required ambient temperature. Humidified air, adjusted to the temperature of the chamber, was pumped through the chamber continuously during body temperature measurements and during the intervals between O_2 consumption measurements. All joeys used in the assessment of the response of body temperature to change in ambient temperature were restrained by surgical tape and fixed to a cork block. Animals used in O_2 consumption measurements were unrestrained within the chamber.

To determine the age at which joeys became able to maintain body temperatures in a cool environment, most joeys were individually contained in the metabolism chamber first at 17·5° C and then at 24° C until their colonic temperatures ceased to change. The final steady-state colonic temperatures were then recorded. Some joeys were assessed only once, at either 17·5° C or at 24° C. The declining colonic temperatures of nine joeys held at 17·5° C were recorded continuously by an implanted thermistor until they reached their final equilibrium values. The body temperatures of some individual joeys were allowed to equilibrate first at ambient temperature of 34° C and then at 37° C. This was to determine the relation between age and colonic temperature in the warm saturated air conditions of the metabolism chamber where conductive, convective and radiative cooling was restricted.

O_2 consumption rates of the 18 individual joeys in one set were measured at an ambient temperature of 20° C and that of another set at 34° C. Each joey was taken directly from its mother's pouch between 09.00 and 10.00 hr and promptly placed in the metabolism chamber. O_2 consumption measurements were usually started about ½ hr after removal of each joey from the pouch and repeated at 1–4 hr intervals until a distinct pattern was obtained. No measurements were taken between midnight and 08.00 hr of the following day. Each measurement of O_2 consumption was the mean of readings taken at 1 min intervals usually for a period between 5 and 30 min. O_2 consumption measurements were corrected to s.t.p. and then expressed as ml./kg.min using the weight of the joey when it was first removed from the pouch (Shield, 1966).

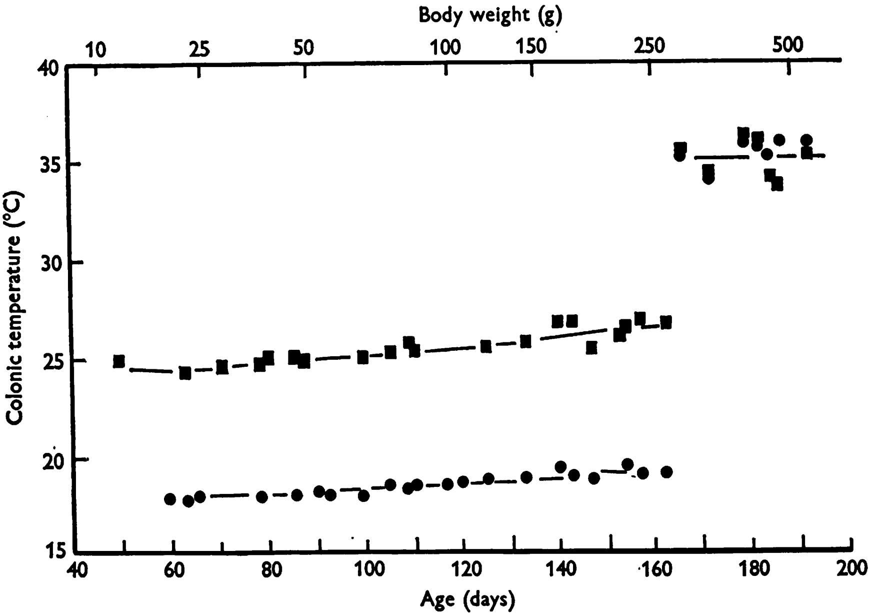

Fig. 1. Steady-state temperatures of pouch joeys aged from 48 to 192 days when kept at humid ambient temperatures of 17·5° C (●) and 24° C (■).

RESULTS

Response of colonic temperature to change in ambient temperature

The relations between age and steady-state colonic temperatures of joeys kept at two cool ambient temperatures are shown in Fig. 1. At an ambient temperature of 17·5° C joeys aged 60 days had colonic temperatures of about 17·5° C. At 162 days of age the steady-state temperature was about 19·1° C. When the ambient temperature was raised to 24° C colonic temperatures rose to about 24·5° C at 60 days and 26·7 °C at 162 days of age. Seven joeys aged between 166 and 192 days maintained their colonic temperatures in the range from 33·8 to 36·2° C when kept at ambient temperatures of 17·5 and 24° C.

The changes in colonic temperatures with time of exposure for nine joeys held at a constant ambient temperature of 17·5° C are shown in Fig. 2. The colonic temperatures of five joeys aged 165 days or less all decreased exponentially with time. The 59-day-old animal reached constant colonic temperature in 2½ hr. The 154-day-old animal took about

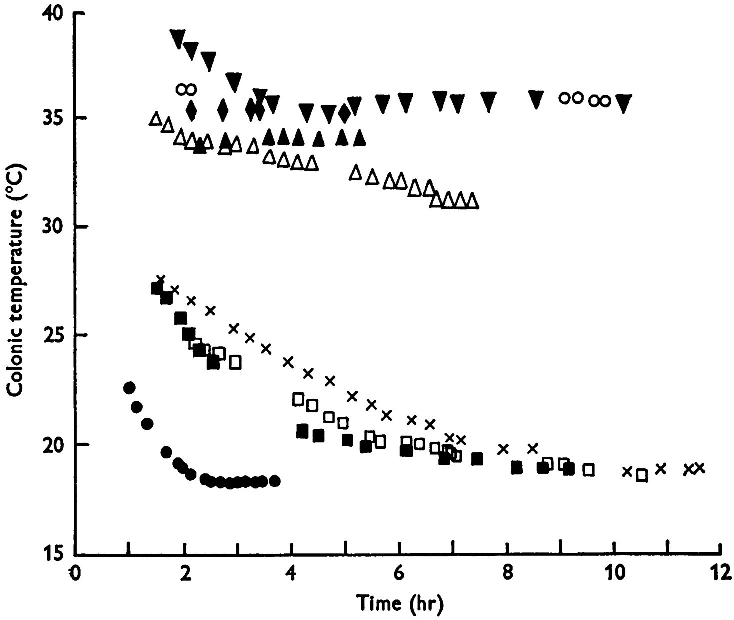

Fig. 2. Cooling sequences of nine joeys aged from 59 to 192 days when transferred from the pouch to a humid ambient temperature of 17·5° C at zero time. ●, 59; ■, 125, □, 143; ×, 154; △, 165; ◆, 166; ▲, 172; ○, 186; ▼, 192 days.

10 hr to reach a steady body temperature. The colonic temperatures of the 165-day-old joey declined to about 32° C in 7 hr. Joeys aged 166 and 172 days held their colonic temperatures constant above 34° C for 4 hr whilst the 186- and 192-day-old joeys maintained their colonic temperatures at about 36° C for longer than 10 hr.

Fig. 3 shows the steady-state temperatures of animals kept at two warm and humid ambient temperatures. At an ambient temperature of 34° C joeys aged 60 days had temperatures of about 34·7° C. Temperatures increased with age until at 192 days of age one animal had a colonic temperature of about 41° C. At 37·5° C the steady-state temperatures were about 38·2 and 40° C in 60- and 120-day-old joeys respectively. At this ambient temperature joeys older than about 130 days died of heat stress.

The rectal and pouch temperatures of eight adult females and the rectal temperatures of their pouch joeys are given in Table 1. These joeys were aged 163 days and older and were therefore close to the age at which they normally become homoeothermic. The rectal temperatures of the mothers (av. 37·30° C) and their own joeys (av. 37·26° C) show little difference but the pouch temperatures average 0·86° C lower than the joeys' rectal temperatures.

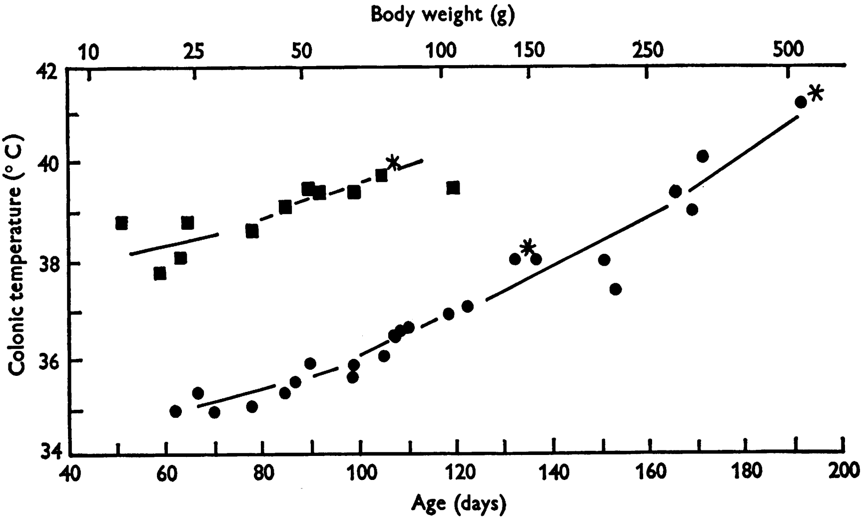

Fig. 3. Steady-state temperatures of joeys aged from 48 to 192 days of age when kept at humid ambient temperatures of 34° C (●) and 37·5° C (■). (* indicates joeys which died soon after removal from the chamber.)

TABLE 1. Rectal and pouch temperatures (°C) of mothers and rectal temperatures of their respective joeys

Joey age (days)	Joey weight (g)	Mother's rectal temp. (°C)	Joey's rectal temp. (°C)	Gravid pouch temp. (°C)
163	294	37·4	37·1	36·6
164	290	37·0	36·5	35·8
164	290	38·3	38·0	37·2
166	370	37·4	37·6	36·0
176	480	36·7	37·3	36·0
178	440	37·3	37·4	36·7
189	457	37·1	36·9	36·7
190	517	37·2	37·3	36·5
Mean values	—	37·30	37·26	36·44

O_2 consumption

Fig. 4 shows the changes with time in mean O_2 consumption rates of the three joeys in each of the six age groups exposed to 34° C. O_2 consumption rates of all joeys except those aged between 120 and 150 days increased during the first 4–8 hr after removal from the pouch. Although the mean values of the several age groups thereafter decreased with time the older joeys generally had O_2 consumption rates about double those of younger animals over the whole period of study of up to 40 hr after removal from the pouch.

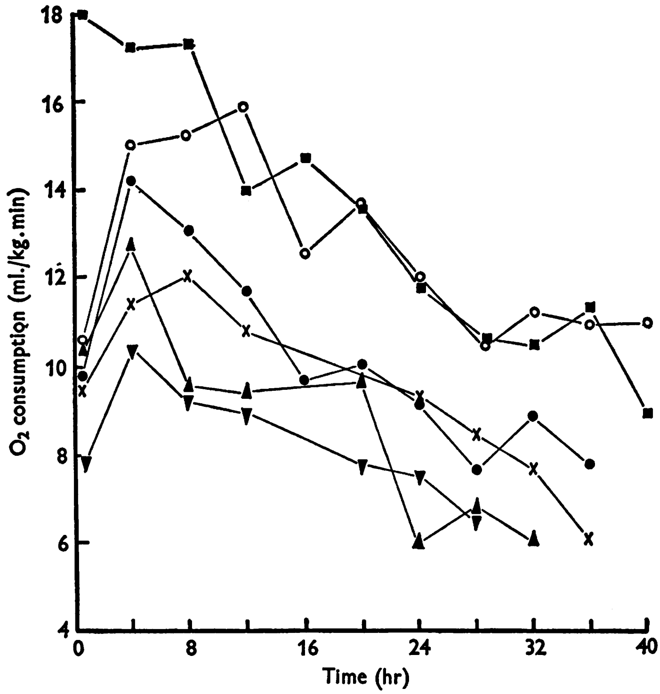

Fig. 4. Mean O_2 consumption rates at 34° C of the three joeys in each of the six age classes of joeys *vs.* time elapsed since removal from the pouch. ▼, 0–30 days; ▲, 30–60 days; × 60–90 days; ● 90–120 days; ■, 120–150 days; ○, 150–185 days.

When kept at 20° C the O_2 consumption of joeys aged 11–90 days declined to about 2·5 ml./kg.min in 1 hr and remained at this reduced level thereafter (Fig. 5). After 8 hr when their body temperatures had equilibrated at about 1–2° C higher than the ambient temperature joeys aged 90–150 days continued to have O_2 consumption rates higher than younger joeys. Joeys aged 169–186 days had O_2 consumption rates higher than those maintained at 34° C. While increasing age did not change the level of O_2 consumption, the length of time they sustained this increased O_2 consumption rate increased. The period of sustained high O_2 consumption increased with age from about 16 hr at 169 days to 76 hr at 186 days of age.

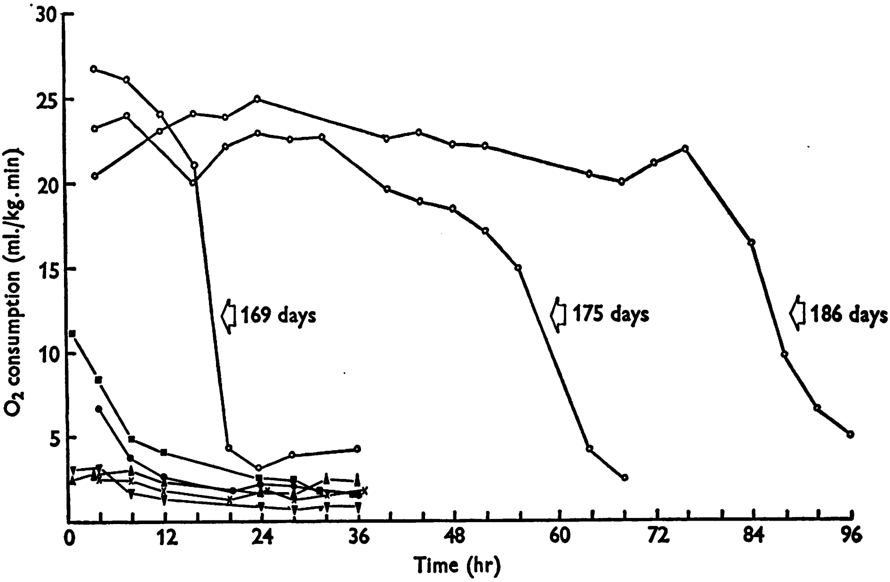

Fig. 5. Mean O_2 consumption rates at 20° C of the first five age classes of joeys (three in each class) *vs.* time after removal from the pouch. ▼, 0–30 days; ▲, 30–60 days; ×, 60–90 days; ●, 90–120 days; ■, 120–150 days. Those animals in the 150–186 days of age class are shown separately (○).

DISCUSSION

The general pattern of steady-state body temperatures in a cool humid environment shows that quokka joeys 166 days and older can maintain their body temperatures at a high and constant value for 5 hr or more. The body temperature of one 165-day-old joey showed a steady decline and reached 32° C after 7 hr. Consequently it just failed to qualify as an homoeotherm. On the other hand a 154-day-old joey cooled to near ambient temperature (20° C) in about 7 hr. The change from the 154-day non-regulated response to the 166-day regulated response must encompass a short period of transition exemplified by the response of the 165-day-old animal. A much larger sample would be needed to demonstrate effectively the variation about the age of transition. It thus appears that joeys become homeothermic 1 month or so before they vacate the pouch permanently.

The pattern of change from the poikilothermic to the homoeothermic state must depend upon whether the development of fur insulation precedes or follows the ability to raise O_2 consumption in the cold. The neonatal rabbit has a very high O_2 consumption rate at 20° C (70 ml./kg.min) but because of inadequate insulation this extravagent use of energy fails to maintain body temperature. With further post-natal development the high rate of cold induced O_2 consumption is reduced concurrently with the acquisition of better fur insulation and the developing young is finally able to maintain body temperature (Hull, 1965). By contrast the underfur of the quokka joey is first apparent at about 125 days of age and by 165 days the joey is fully furred (Shield, 1961). During most of this period there is no concomitant increase in body temperature above ambient nor is there any increase in O_2 consumption when subjected to cool ambient temperatures. However, between 154 and 166 days there is an almost simultaneous increase in ability to maintain high body temperatures and to increase O_2 consumption in the cold. In confirmation of the fully insulated state of the 165 day old joey there is no decrease in O_2 consumption of older joeys when left at the same cold temperature as would be expected if insulation was being further increased during development. However, during this initial stage of homoeothermy the endurance of high O_2 rates at 20° C is extended from 16 hr at 169 days of age to 76 hr at 186 days.

The mechanism underlying this sudden increase in energy production between the 154th and the 169th day of development is unknown. It cannot be the result of the abrupt development of the shivering response as shivering was first noticed in a 121-day-old joey (Shield, 1961) but may be a manifestation of an increase in shivering intensity during ontogeny. It is probably aided by the general increase in metabolic rate with age as this study shows that older joeys maintain a metabolic rate of about twice that of younger joeys over a period in excess of 28 hr. Also, it may be related to the ability to release sufficient thyroid hormone in the circulation when induced by cold ambience, as Setchell (1974) has shown that the response of high O_2 consumption rates in the cold is a function of the growth of the thyroid gland in the marsupial *Macropus eugenii*. The American marsupial opossum (*Didelphis marsupialis virginiana*) has a similar development pattern of homoeothermy to that of the quokka. Morrison & Petajan (1965) showed that opossums 60 days of age kept at 24° C had colonic temperatures near ambient but had colonic temperatures of 35° C at 90 days of age. Apparently in this marsupial species also the increase in fur insulation precedes the ability to generate heat.

For the quokka joey incubated in the maternal pouch there is, however, no apparent metabolic economy in the early development of fur insulation (when compared with the rabbit). When kept in a warm and humid metabolism chamber which denies conductive, convective or evaporative heat loss older joeys apparently have a problem in disposing of their metabolic heat. At 37·5° C (approximately pouch temperature) with high humidity all joeys older than about 130 days increased their body temperatures to the lethal level of about 42° C. However, when in the pouch older joeys do maintain rectal temperatures near those of their mothers and they must therefore obtain access to an effective heat sink which is unavailable when thermally insulated and enclosed in a humid metabolism chamber. Two such avenues of heat loss are available to the pouch joey. The first avenue of heat loss is conductive. For young hairless joeys, contact with the pouch epithelium probably affords a good thermal conduction and transfer of the joey's metabolic heat to the mother. In older joeys the damp pouch tends to lower the insulative property of the fur and ensure a better thermal contact with the mother which serves as a conductive heat sink. A second avenue of heat loss is evaporative. Younger pouch joeys in the 120- to 150-day range sometimes assume a posture which enables only their nostrils to protrude from the gape of the pouch. Older joeys may be seen with their heads constantly protruding. Obviously, joeys aged 120 days and older do breathe cool dry air and not humid pouch air and evaporative cooling through respiratory water loss may account in part for their ability to keep their body temperatures at about 37·5° C.

The foregoing results do not allow the quantitative partitioning of heat transfer between these two sinks, but whereas the conductive transfer probably remains constant or even declines (because of a smaller surface/volume ratio) during development the evaporative component probably increases. The developing joey will therefore most probably be progressively forced to rely more and more on respiratory heat loss to maintain a normal body temperature. Respiratory discomfort and finally mutual thermal intolerance between mother and joey may then lead to the joey's first ventures outside the pouch.

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